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Looking for unity in diversity: human cooperative childcare in comparative perspective

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Abstract

Humans engage in cooperative childcare, which includes some elements not found in other animals, such as the presence of post-reproductive helpers, extensive food sharing among adults, and a pervasive sexual division of labour. In animals, cooperative offspring care has typically been studied in two different contexts. The first mainly involves helpers contributing care in cooperatively breeding family groups; the second context is allomaternal care in species usually not categorized as cooperative breeders (e.g., plural and communal breeders, often without male care). Comparative analyses suggest that cooperative breeding and allomaternal care in plural and communal breeders have distinct evolutionary origins, with humans fitting neither pathway entirely. Nevertheless, some critical proximate mechanisms of helping, including hormonal regulators, are likely shared across species. Other mechanisms may vary amongst species, such as social tolerance, proactive prosociality or conditional mother-infant bonding. These are presumably associated with specific details of the care system, such as whether all group members contribute, or whether mothers can potentially raise offspring alone. Thus, cooperative offspring care is seen in different contexts across animal lineages, but may nonetheless share several important psychological characteristics. We end by discussing how work on humans may play a unifying role in studying cooperative offspring care.

Running head: Elements of cooperative breeding

35

36 **Key words:** cooperative breeding, allomaternal care, comparative analyses, human
37 evolution

1. Introduction

Evolution involves descent with modification, and therefore generally leads to increasing morphological, physiological and behavioural diversification. Sometimes newly evolved, derived traits in one lineage are functionally similar to traits in other lineages, a phenomenon called evolutionary convergence. Examples include the evolution of flight, warning coloration, complex eyes (1), or cooperative breeding (2, 3). However, the underlying genetic basis of these convergently evolved traits will only rarely be identical (1).

Tinbergen (4) famously distinguished between proximate and ultimate aspects of behaviour, implying that selection for a function is actually selection of a mechanism. Thus, despite differences in the genetic foundation, it is not implausible to expect similarity at higher levels of proximate causation. For behavioural traits we may therefore ask whether the underlying motivations or psychological predispositions (i.e. an individual's attitudes towards sets of objects or behavioural options, typically reflected in explicit decision-making (5)) are similar enough to warrant giving them the same label, at least in members of the same broad lineage.

Here we examine the case of cooperative offspring care. Although definitions of cooperative breeding have drifted over time (6-8), it is usually defined as conspecifics helping parents raise their young (2, 8, see also below). By this definition, humans are cooperative breeders, but our cooperative breeding almost certainly arose from a different ancestral state (9, 10) than it did in birds (3) and other mammals (2), amongst which it evolved independently multiple times and largely from similar ancestral social systems. Moreover, despite the variability amongst and between birds and mammals, the human version differs in so many respects from both (elaborated below) that various experts have argued humans should not be given the same label (11, 12). This debate suggests it is important to recognise the potential heterogeneity of cooperative offspring care in different species or lineages.

Indeed, one possible reason for confusion about the state of humans versus the other cooperative breeders is that allomaternal care is observed in two distinct contexts (Figure 1). The first context is cooperative breeding in species with biparental care, either birds or mammals (including callitrichid primates). Research here often focuses on what makes helping by non-reproducing individuals adaptive (8). This work considers several forms of helping behaviours, such as incubation, sentinelling, baby sitting, provisioning or carrying, but major foci are the role of kin

selection (13, 14), and cases where helpers contribute to rearing non-kin or distant relatives (15).

The second context is allomaternal care in group-living mammals with plural breeding, such as elephants, coatis, dolphins, sperm whales and many primates, with quite variable paternal involvement. Researchers ask how much of which kind of help a breeding female receives in the form of provisioning, infant carrying or babysitting, and what benefits she derives from this (16-19). Importantly, this perspective acknowledges that help can be vital to immatures even if the costs to helpers are modest, as when an experienced female elephant helps the calf of another mother to move out of a ditch from which it could not escape without help (20). This kind of allomaternal care overlaps with communal breeding, where reproductive females help each other (16), but it is perhaps best to separate the non-nursing care considered here from allonursing, which has almost certainly evolved independently (21, 22) and only involves adult females that currently have dependent offspring. In sum, allomaternal care is seen in both cooperative and non-cooperative breeders, and the form, function and proximate regulation of the behaviours involved may differ as well.

The aim of this paper is to examine to what extent shared offspring care in humans and other mammals or birds represents overlapping sets of traits, each of which may be homogeneous in terms of function and regulation. Ultimately, we wish to assess the extent to which major psychological predispositions of humans that make us different from the other great apes can be traced back to the evolution of the human-specific form of cooperative breeding, as postulated by the cooperative breeding hypothesis for human cooperation (17, 23).

We begin with an overview of cooperative offspring care in birds and mammals, and then present the human case. Then, we discuss the differences in the ancestral states between cooperative breeders and species with allomaternal care that are usually not considered cooperative breeders. We find that cooperative offspring care has multiple independent origins and varies in form and function. We will see that many of the distinct elements of extensive allomaternal care in cooperative and independent breeders share hormonal and psychological mechanisms, despite having different histories and somewhat different functions.

2. Cooperative offspring care: basic description

Most definitions of cooperative breeding describe systems where helpers assist a breeding pair in raising offspring (7, 8), and thereby exclude most species in which allomaternal care but no male care is found (but see 24, 25). In species where non-parents help, it is most often a family or extended family affair where offspring remain with their parents beyond independence and assist them in raising younger siblings (26). Nevertheless, it is quite rare for helpers to only direct their care towards offspring of their own parents, but they direct it towards offspring with varying degrees of kinship. In birds, helpers are usually sexually mature (3); in mammals they are commonly juvenile (7). Interestingly, in almost all birds where young remain in the family until the next breeding season, they act as helpers (3). In contrast, as elaborated below, in most mammals where young remain with their mother after weaning they do not provide allomaternal care (27), showing that delayed dispersal in mammals does not inevitably lead to cooperative breeding. Estimates of the prevalence of cooperative breeding vary because tropical species remain poorly studied (28), but it appears more common in birds than in mammals: about 15-25% of bird species (3, 8, 28) versus about 2.5-3% or more of mammal species (2, 25, 29). There is considerable variation on the theme of cooperative families (8). For instance, reproductive skew can be moderate or extremely high (14), and in some species, cooperative breeding is facultative whereas it is obligate in others.

Humans spent most of their evolutionary history as nomadic hunter-gatherers or foragers (30). The rearing system of foragers involves extensive allomaternal care (16). Fathers or other adult men often make major energetic contributions (31, 32), as do grandmothers (33), though generally less than fathers or men generally (34). Grandmothers and older children provide babysitting services (35), either in the band's camp or during foraging (36), which allows mothers to forage more or more efficiently. The energetic contributions of the immatures, however, are modest (37), largely because the skill-intensive foraging niche is mastered only late during ontogeny. Communal nursing is common, but generally involves close kin (38), and the caloric transfers provided by fathers and grandmothers are far more important. Taken together, mothers receive abundant help by allomothers. This includes significant help from non-breeding helpers, both from pre- and post-reproductive age categories, and all helpers flexibly complement each other's contributions. As the saying goes, it takes a village to raise a child.

Help does not merely flow towards immature offspring, however. There is also systematic adult-adult food sharing. First, within families, men and women forage on distinct sets of food items (39), which they subsequently share or exchange. Second, meat and honey, largely acquired by men, are also shared widely in a camp, reflecting the strong male bonds in a foraging band (40).

Despite cooperative breeding, reproductive skew in forager societies is modest. The social unit of foragers is a multi-level system of bands within a larger macro-band or community (41). Crucially, each band contains multiple, interdependent families as well as unattached adults. Due to pair bonds between unrelated individuals, different families are not necessarily all closely related to each other (30, 42). As a result of opportunistic dispersal and pair bonds, relatively few dyads are at the full-sib level (42). Much support therefore goes to non-kin, because of extensive between-family sharing. However, because the sharing provides temporal stability at various time scales (43), bands would rarely be viable if they contained only a single family.

In sum, in humans the cooperative family element is complemented by male-male sharing of valuable foods, extensive care by post-reproductive women and two-way sharing within the pair-bond, plus some sharing and caring by unmarried adults. Thus, in humans the help is not just directed at immatures but also at adults of either sex.

3. Evolutionary origins

Here, we briefly discuss the evolutionary origins of help in rearing offspring, distinguishing cooperative breeding (Figure 2a and 2b), allomaternal care in plural breeders (Figure 2c), and the human system (Figure 2d).

3.1 Cooperative families in birds and mammals

Cooperative breeding among birds most likely arose in two steps (3). First, in pair-living species, offspring began to stay with their parents beyond nutritional independence, leading to family living. The conditions favouring family living were thought to be high risk of predation and opportunities for skill learning for the immatures (44-46). Second, where in such family groups young were still around during the next breeding attempt, they typically helped their parents rearing the next brood(s) despite already being of reproductive age. This was presumably facilitated

by less predictable food supplies through increasing environmental variability (47), and thus steeper fitness benefits from receiving help.

Cooperative breeding among pair-living mammals also likely evolved in two steps. The transition towards pair living appears less prevalent in mammals than in birds because male mammals can less readily assist their lactating females in raising offspring through provisioning. This transition towards pair living may be facilitated by different evolutionary drivers (48, 49). Among infant-carrying primates, for instance, social units generally contain both sexes, presumably to reduce infanticide risk, so when groups become smaller, associated pairs may remain (50, see also 51, 52, for a summary of the debate regarding the role of infanticide for pair living). In mammals, not all males living in pairs engage in direct infant care, and young often disperse late enough to be able to help rear the next set of young (26.6% in mammals; 11.1% in birds [M.G., unpubl data.]), but they usually don't help. The first step towards cooperative breeding in pair-living mammals therefore probably was that males began to provide care (49). Secondly, this allowed females to increase their reproductive effort, which made it advantageous for older young to begin helping to rear their younger siblings (2). This final transition towards help by offspring may have been facilitated, as in birds, by an increase in the variability in food availability (29).

In sum, in birds, where 55% of species are pair living (3), family living appeared to be the critical precondition for the transition to cooperative breeding. In mammals in contrast, where 95% of species show female-only care (49), it was more likely male parental care and the accompanying increased female reproductive investment that was the critical precondition (Figure 2, a and b). However, in both birds and mammals, high average relatedness in the social units was a precondition and thus kin selection responsible for the evolution of cooperative breeding in most cases (2, 3).

3.2 Allomaternal care without cooperative breeding

In a range of species, help is provided by pre-reproductive helpers, breeding is plural, and male care is often absent. Allomothers may protect and babysit infants, which allows mothers to forage more efficiently. Examples include elephants (20), sperm whales (53), and primates, where non-mothers, including other females that are not close relatives, may show extensive infant carrying and babysitting (16, 18, 54).

Females make up the most common class of allomothers, especially but not exclusively adolescents (16).

Although the actual helping effort is often modest, it may have a major impact on the survival of the offspring (55) or the mother's rate of infant production (19), as confirmed by comparative studies (56, 57). This explains why effective allomaternal help can evolve despite lower relatedness between helpers and offspring, as in non-monogamous species (Figure 2c).

3.3 Humans

Palaeo-anthropologists assume that the earlier forms of the genus *Homo*, around 2 Ma, lived in large mixed-sex groups, just like our closest-living relatives (10). We can conclude this, for instance, because no terrestrial or semi-terrestrial primate species is socially monogamous (58). In later forms, we see evidence for communal defence against predators (59) as well as cooperative hunting, as suggested by the hunting of large bovids (60). It is therefore most likely that our evolutionary history never showed the state of isolated dispersed, territorial male-female pairs that set the scene for cooperative breeding in other mammals and birds. Cooperative breeding in our lineage therefore had likely evolved along another path (9).

Any reconstruction must remain speculative at this stage (10, 61), but the elements listed earlier almost certainly evolved partly independently. As suggested in Figure 2d, likely crucial early elements were the presence of male-male bonds and non-exclusive male-female friendships, the increasing difficulties of immatures to feed themselves (and thus steeper fitness benefits of provisioning them), and the gradually increasing difficulty of giving birth, which may have led to the evolution of midlife menopause and thus provisioning and helping by grandmothers (10, 59, 62). Critically, the extensive help and sharing seen in humans seems not due to unusually high relatedness between helpers and offspring (9). Rather, human immatures could not be reared successfully without extensive allomaternal care and interdependent adult human foragers could not survive without the extensive within-band sharing (30, 43).

4. The major elements of cooperative offspring care

The unexpected heterogeneity in cooperative offspring care (7, 8) suggests it might be useful to examine the broad phenomenon as a bundle of potentially

independent elements. In Figure 3, the white block contains the two core components of cooperative breeding in birds and mammals: help by breeding males and help by non-reproducing close kin. As noted above, in mammals, we can find cases where the breeding males do not help, but others provide care (18, 21). In addition, help may also be provided by others than older siblings or the sire (light grey) (15). While this is common in humans, it is also common in other species, and may reflect the need for individuals to be members of a group rather than solitary floaters, which can have substantially lower survival (63). In this case, helpers are not always close kin of those they help, and we may expect a pay-to-stay system (64). Alternatively, helping relatives rearing offspring may be the best option to maximize inclusive fitness in a given situation. For instance, when their own nest fails, white-fronted bee-eaters and long-tailed tits provision the nestlings of relatives (65, 66). Helping by unrelated individuals may be even more common than expected when the focus is not exclusively on provisioning (21).

Another additional element of cooperative breeding can be co-breeding by males. Especially in mammalian carnivores, some birds, and callitrichid monkeys, paternity is not always monopolized by a single male (15, 67-69). This may reflect concessions to maintain critical collective action, as in social hunters that require more than two hunters to kill or defend prey (70), or the need for multiple helpers, as in obligate cooperative breeders, which means that a single breeding pair cannot establish a new group (71). Some tamarin species, for instance, may fail to breed as pairs and are therefore routinely polyandrous (69, 72). Humans are quite different, because all men in forager groups are pair-bonded, at least in principle. Yet, this may merely be on one endpoint of a continuum because in areas of low productivity marriage arrangements may become polyandrous (73).

The elements in the lower row of Figure 3 are not traditionally considered part of cooperative breeding (see also section 2). In many group-living mammals, but especially primates (21), breeding females receive some allomaternal help (i.e., infant carrying, babysitting and sometimes allonursing), usually by kin that are selective in their help (e.g., 74). Thus, female co-breeding is frequently found in allomaternal care systems, but the co-breeding found in humans is unusual due to the intensity of allomaternal care.

Premature menopause, and thus the presence of non-reproducing older females (grandmothers), is found in humans but has also been reported for some

whales, e.g., in orcas. However, because menopause in orcas should probably not be considered allomaternal care (75), it may well be that grandmothering with menopause is uniquely human.

At least two elements, finally, appear uniquely elaborated to humans. The first is systematic male-female food sharing, a reflection of the sexual division of labour. Although provisioning of the female by the male is also seen in various cooperative breeders, especially during incubation in birds (76), this provisioning is not reciprocal. The second element is systematic, reciprocal sharing of valuable foods by a local band's men (77), which is an expression of the male-bonding component of human social organization. Male bonding is also seen in chimpanzees, lions, or raptors, but they show opportunistic sharing around a kill (78-80) rather than the transport of the quarry to a central home base and thus proactive sharing, as seen in humans. Thus, again, this element may be uniquely human, although the provisioning of adult African wild dogs that remain in the den to guard the young while the rest were out to hunt may be an intermediate case (67).

Because the patchy distribution of these elements suggests independent origins, it may be worth asking whether they are also regulated by distinct processes. However, due to the great similarity in the actual actions involved, they may actually have come to share proximate mechanisms. We now turn to this question.

5. Proximate mechanisms of cooperative offspring care

As implied by Tinbergen's framework (4), selection for allomaternal care behaviours requires selection on a proximate mechanism, such as a genetically based hormonal regulatory system, which can bring about changes in psychological preferences and predispositions. Here, we ask whether these mechanisms are characteristic for cooperative breeders in the commonly accepted sense or extensive allomaternal care per se, and to what extent variation in the elements of cooperative breeding discussed above (Fig. 3) might influence which proximate mechanisms are selected for in a given species.

5.1 Hormonal mechanisms

At the hormonal level, the regulatory system involved in maternal behaviour seems also involved in allomaternal behaviour by male breeders, kin helpers, and other allomaternal care providers (81-84). For instance, in meerkats, peripheral

administration of oxytocin increases provisioning and affiliation with pups (85). In marmosets, oxytocin increases not only in mothers after the birth of infants but in all group members. It is also associated with infant licking and food sharing (86) and reflects social bonds among adults (87). The oxytocin system also seems involved in human grandmothering (88). Likewise, increased levels of prolactin are associated with a higher helper effort in Florida Scrub jays (89), meerkats (90), and marmosets (82, 91). Importantly, the same pattern also holds for allomaternal care in plural, non-cooperative breeders (92).

Hormonal systems regulating maternal behaviours often also have other sex-specific reproductive functions, which might interfere with the reproductive functions of the opposite sex. Some differences in the hormonal regulation of male vs. female allomaternal care must therefore be expected (93-95). Furthermore, the necessity to be physiologically ready to reproduce independently in case a breeding opportunity arises will impose further constraints (96, 97). In fact, trade-offs between infant care and independent reproduction may predict species differences in helping. For instance, these trade-offs may bias against helping in species with year-round nesting but not in seasonal species (98). In the latter, individuals who did not manage to breed will anyway have to wait until the next year to mate and therefore the reduced testosterone levels associated with helping (96, 99) will not compromise mating success in the following year.

Neuro-endocrine mechanisms often regulate behaviour by modulating psychological predispositions and motivations which we will discuss now. In the case of helping behaviour, these may include social tolerance, spontaneous or proactive prosocial predispositions, as well as the readiness of mothers to share their offspring and to bond with a newborn infant.

5.2 Psychological adaptations in helpers

The most common helping behaviours are provisioning, protection and vigilance, and in primates, infant carrying (8, 21). All require high social tolerance towards the offspring. Whenever these behaviours have to be coordinated in close proximity to other group members, high tolerance towards adult group members is also required, such as around the nest in birds or around and inside the den in burrowing mammals. In species where infants are carried and thus transferred from one caregiver to another, all potential carriers must be highly tolerant. Both

observations from the wild (69, 100, 101) and empirical evidence in captivity (102-104) suggest the amount of allomaternal care is indeed correlated with group-level social tolerance in primates. Important in the context of this paper, what is decisive is the extent of allomaternal care, rather than whether or not a species qualifies as cooperative breeder. We are not aware of similar comparative analyses for a link between social tolerance and cooperative breeding in other lineages, although in birds, high social tolerance near the nest likely determines whether species breed cooperatively or not (105).

Living in larger groups with high reproductive skew increases competition between group members for breeding slots, which may lead to high degrees of context-specificity of social tolerance. For instance, in callitrichid monkeys (97, 106), the high social tolerance during everyday activities is punctuated by episodes of intense competition when breeding vacancies become available, a pattern also found in cooperatively breeding apostlebirds (107, M.G., unpubl data) and acorn woodpeckers (108). In very large groups with extreme reproductive skew, one possible way of dealing with increased competition is to restrict tolerance mostly to offspring. This, however, requires that helping can be organised in a way that minimizes the need for close behavioural coordination between adults.

Social tolerance is a necessary precondition for helping, but not sufficient: additional psychological mechanisms are necessary. One possibility is that each of the specific helping behaviours of a given species is the result of automatic triggering by specific cues (e. g., feeding triggered by begging cues, or caring for larvae by olfactory cues). This type of regulation can be nonflexible and prone to misdirected offspring care (see 24). Alternatively, the helping behaviours may be regulated more generally by a psychological prosocial helping disposition. The latter seems to be the case in at least some mammals. For instance, oxytocin is involved in the regulation of *multiple* infant care behaviours (e.g. food sharing and infant licking in marmosets (86)), a variety of other cooperative behaviours such as sentinel behaviour and digging (meerkats; 85), as well as in experimentally assessed proactive prosociality between adults (marmosets: 109).

For primates, experimental comparative evidence over a large number of species supports a link between proactive prosociality and cooperative offspring care (103). Again, interspecific variation in proactive prosociality was better explained by the extent of allomaternal care rather than qualifying as a cooperative breeder or not

as, as was the case for tolerance. Such a link has been questioned, in particular for non-primate species (see (110, 111) but also (104)), but recent evidence from dolphins (112) and corvids (113) suggests that it may not be limited to primates. More comparative data will help to further narrow down in which lineages and under which conditions allomaternal care is linked with social tolerance and proactive prosociality.

Both in the wild and in naturalistic situations in captivity, proactive food sharing in callitrichids is predominantly directed at immatures (114), which may appear conflicting with experimental evidence suggesting proactive prosociality between adults as well. However, even food sharing with immatures is not indiscriminate, but increases when food is difficult to obtain for the immatures (Leontopithecus chrysomelas: 115, Saguinus oedipus: 116, Callithrix jacchus: 117). In experimental prosociality tasks, food can not be obtained independently at all by potential recipients, and it is in exactly this situation where proactive prosociality between adults is measured. Such situations may be rare in naturalistic conditions, where proactive prosociality between adults is therefore more likely involved in facilitating cooperation, as in collective action and cooperative behaviour in various contexts, including cooperative food harvesting, vigilance and other forms of predator protection, territorial and resource defence (100, 118), but also cooperative communication (119). In fact, cooperation tasks reveal that callitrichids are more likely than capuchin monkeys, chimpanzees or orangutans to maintain high levels of cooperation even if for some time they don't obtain a reward for it (120). This corresponds to the situation in humans, where prosocial tendencies assessed in experimental tasks (121) likewise do not imply that all resources are shared with others all the time, but that this predisposition is context dependent and involved in facilitating a broad range of cooperative behaviours. In fact, due to more complex cognitive abilities in humans, and perhaps supported by uniquely human evolutionary processes such as cultural group selection, this may well have given rise to some of the uniquely derived human features such as large-scale cooperation and language (17).

5.3 Psychological adaptations in mothers: tolerance and conditional mother-offspring bonding

Psychological adaptations may not only be required in helpers, but also in mothers. First, mothers have to tolerate others around their offspring, which is not

obvious. Young primate females, for instance, often show a high motivation to interact with immatures, but may also leave the infants behind or even abuse them when their interest wanes. These cases are best described as kidnapping and do not benefit the infant (16, 122), although mothers may allow their kin to handle infants (123). Thus, maternal tolerance towards others is kin-biased (16). However, in classic cooperative breeders, such as callitrichids, selective intolerance toward potentially breeding females is also found when helper females potentially start breeding and help is limited (86, 97).

Second, in specialized cooperative breeders where raising infants without help is not possible, a mother's readiness to invest in the offspring may be contingent on the perceived availability of allomaternal care. When females perceive a lack of help, they may choose not to invest in the current offspring. At the proximate level, this may be mirrored in conditional postpartum responsiveness of mothers to infants, as proposed for humans and other cooperatively breeding primates, which can prevent mothers from immediately bonding with the new-born and thus enables her to eventually reject it (124).

Since more systematic reliance on helpers can only evolve once mothers have acquired some levels of tolerance towards potential allomothers, together this supports the crucial role of kin selection early in the evolutionary trajectories towards allomaternal care in all contexts, including cooperative breeding. In contrast, the conditional investment by mothers in their new-born offspring, depending on the availability of help, must be a more derived adaptation, only expected in obligate cooperative breeders.

6. Discussion

This special issue addresses the question of how studying humans can help identifying biological fundamentals. The obvious answer must be that no one species is more important than another one, because fundamental biological processes can only be established based on broad patterns observed across species. Nonetheless, humans often appear unique among animals in many ways, which can lead to a new perspective on related phenomena in animals. We have focused on human cooperative child care, and doing so indirectly shed new light on the variability of shared offspring care in animals.

444 Consideration of the human form of cooperative breeding led to the realization
445 that allomaternal care is seen in two distinct contexts: cooperative breeding, where the
446 modal pattern is that offspring help their parents raise younger siblings, and
447 allomaternal care in independent breeders, where help tends to be less spectacular and
448 pervasive. In humans, we see both elements, plus others, such as male bonding, which
449 led to a male predisposition to share food with allies, and a pronounced sexual
450 division of labour in the pair bond.

451 The evolutionary origins of cooperative breeding and allomaternal care appear
452 clearly distinct, as do the evolutionary trajectories that led to cooperative breeding in
453 birds and mammals (2, 3). In birds, family living is a critical precondition, whereas in
454 mammals it is male care. In the human case, we find both elements, but also midlife
455 menopause and male bonding, although it is difficult to assess in which order these
456 derived traits evolved. However, despite these distinct evolutionary histories, strong
457 convergences nonetheless appear to exist at the proximate (hormonal) level.

458 As to psychological predispositions, comparative primate data arguably
459 support a direct link between allomaternal care and social tolerance and proactive
460 prosociality. For researchers interested in the evolution of prosociality and tolerance
461 in humans, primates are most relevant, given the importance of path-dependence in
462 evolution. Whether such a link also exists in other lineages remains an empirical
463 question, but its pursuit is one example in which research on humans can give rise to
464 efforts to establish biological fundamentals. The same comparative work on primates
465 also revealed that the overall extent of allomaternal care, rather than being classified
466 as a cooperative breeder or not, is more important for the prevalence of these
467 psychological predispositions. These results show that it is fruitful to combine the
468 perspectives of cooperative breeding and allomaternal care, which became necessary
469 because humans show a combination of both.

470 In sum, studying the role of cooperative breeding in human cooperation not
471 only led to new hypotheses and insights regarding human evolution but can also
472 impact research on biological fundamentals in other animals. In particular, it can lead
473 to a better integration of the rather separate research traditions of cooperative
474 breeding and allomaternal care, raises the issue of lineage specificity of biological
475 processes, and offers a test case for how deeply shared proximate convergence can be
476 found in functionally convergent traits.

477

478 **Ethics statement**

479 This review contains no original data.

480

481 **Data accessibility statement**

482 Does not apply

483

484 **Competing interests statement**

485 We declare no conflict of interests.

486

487 **Authors' contributions statement**

488 JB, MG and CvS wrote the paper.

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Figure 1.
Contexts in which cooperative offspring care in animals is typically studied.

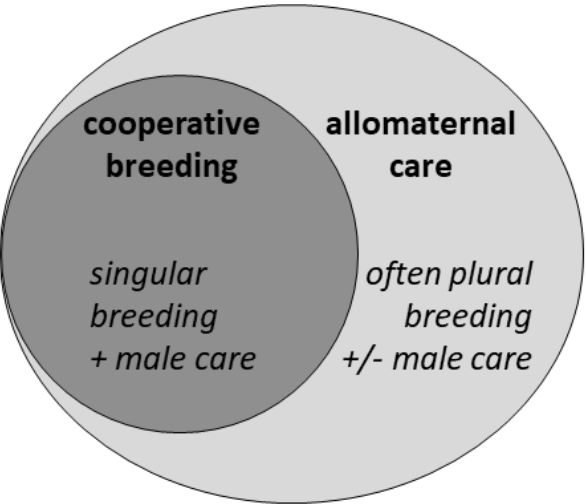


Figure 2.

The evolutionary pathway towards classic cooperative breeding (CB) in birds (a) and mammals (b), and towards allomaternal care in plural breeders (c) and cooperative breeding in humans (d).

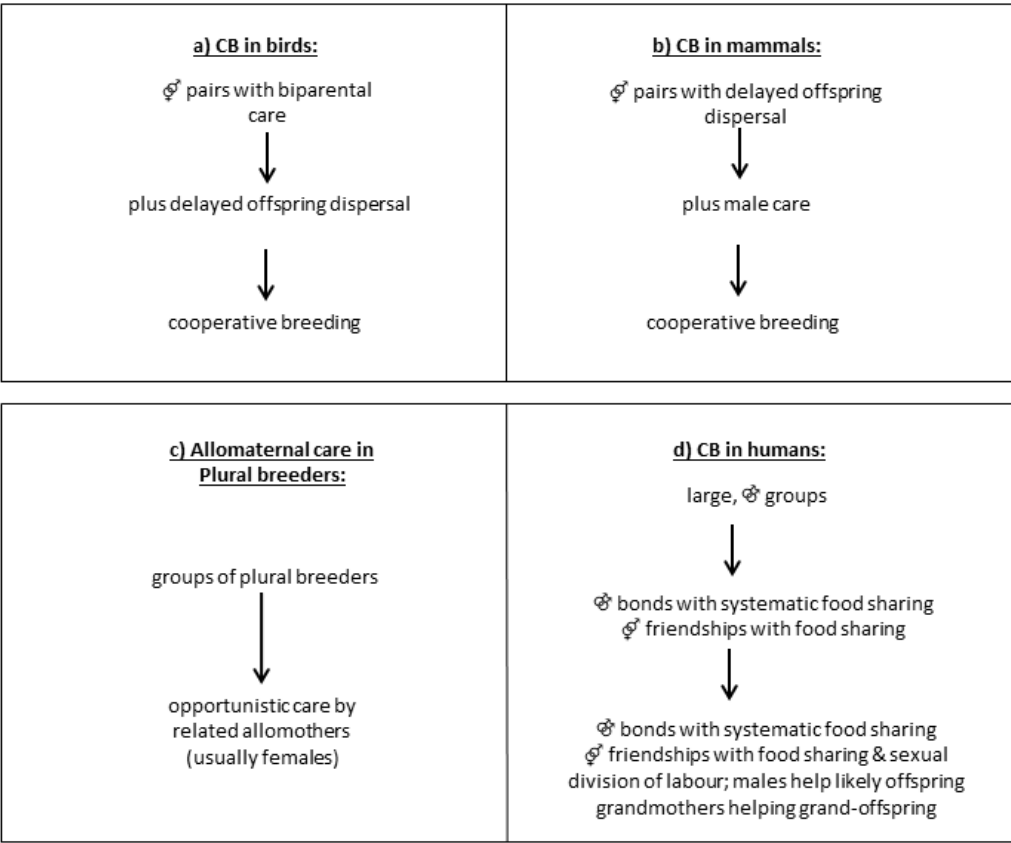


Figure 3.

The main elements of cooperative offspring care systems. Entries in the first row are the major elements of classic cooperative breeding (cooperative families); those in the second row are not.

Help by non-reproducing close kin	Help by male breeder	Help by others (non-kin)	Co-breeding males
Co-breeding females	Help by grandmothers	Systematic male-female food sharing	Systematic male-male food sharing